

Species concepts

by Robert M. Zink

It is difficult to imagine a concept that impinges on more biological research than that of the species. Most biological studies refer to their subjects as members of some species (Hauser 1987). We are often taught that species are the only units in the classificatory scheme that exist independent of taxonomists; i.e. species are real. Given the importance of species in theories about evolution, ecology, and behaviour, faunal lists, and for communication of our understanding of biodiversity, lack of agreement about how biologists define species is surprising.

The species debate was evident in Darwin's time (1859), and has escaped general resolution in the last 130 years, except perhaps for the fact that most agree that the word species derives from Latin meaning 'appearance' with a secondary meaning 'kind'. Today the literature is replete with different definitions (Table 1). Some (e.g. Endler 1989) suggest that different species concepts are needed to study different evolutionary processes. Paleontologists must cope with incomplete fossil histories and absence of information on mating tendencies (Wiley 1978). Botanists must deal with reticulation, recognizing that a large percentage of all plant species, perhaps 50% or more, is of hybrid origin (Cronquist 1978). A large number of biologists claim to follow the so-called biological species concept (BSC; Mayr 1942), in which reproductive isolation is viewed as the crux of speciation. In the past 15 years, those coming from a background in phylogenetic systematics, or 'cladistics', have made substantial contributions to the debate about species, and have penned a number of 'phylogenetic' species concepts (Cracraft 1983, de Queiroz & Donoghue 1988, Nixon & Wheeler 1990). Although argument over species concepts has persisted for more than 100 years, it is my thesis in this paper that the contributions from phylogenetic systematics have substantively changed the nature of the debate. Furthermore, it is my opinion that the long-entrenched biological species concept is losing favour in ornithology (Zink & McKittrick 1995, Hazevoet 1996) and elsewhere (Mallet 1995).

Comparison of the species concepts given in Table 1 is beyond the scope of this review. Instead, I will contrast the biological species concept and a phylogenetic alternative. The reason for doing so is that I believe that the current debate about species concepts has come to focus on whether to give primary emphasis to a process, such as mate choice, or to correct representation of evolutionary patterns, such as those recovered by direct analysis of characters (Graybeal 1995). These two conceptual positions are embodied in the BSC and a PSC, respectively. Here I review each concept, noting some perceived strengths and weaknesses (Tables 2, 3).

The biological species concept has a long history in ornithology (Haffer 1992, Amadon & Short 1992, Bock 1986, Hauser 1987). A perceived advantage of this concept is that it is 'biological'. By

TABLE 1
Some species definitions or views on species

"No one definition has as yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species." (Darwin 1859)

"A species is a set of populations capable of combining with each other but not with other similar sets of populations on the basis of affinity and co-direction in ecological specialization." (Shaposhnikov 1966)

"A species is a group of organisms not itself divisible by phenetic gaps resulting from concordant differences in character states (except for morphs such as those resulting from sex, caste, or age differences), but separated by such phenetic gaps from other such groups." (Michener 1970)

"We may regard as a species (a) the smallest (most homogeneous) cluster that can be recognized upon some given criterion as being distinct from other such clusters, or (b) a phenetic group of a diversity somewhat below the subgenus category, whether or not it contains distinct subclusters." (Sneath & Sokal 1973)

"Somit ist die Art als das Kollektiv von Lebewesen zu bestimmen, das gemeinsam eine ökologische Nische behauptet." (von Wahlert 1973)

"Species may then be defined as groups of phenetically similar populations that have the capability to interbreed, and share similar ecological characteristics." (Doyen & Slobodchikoff 1974)

"Species, then, are the most extensive units in the natural economy such that reproductive competition occurs among their parts." (Ghiselin 1975)

"A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from any other lineage in its range and which evolves separately from all lineages outside its range." (Van Valen 1976)

"Species are the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means." (Cronquist 1978)

"A species is a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate." (Wiley 1978)

"A 'species' is merely a population or group of populations defined by one or more apomorphic features, it is also the smallest natural aggregation of individuals with a specifiable geographic integrity that can be defined by any current set of analytical techniques." (Rosen 1979)

"A species is a group of animals or plants all of which are similar enough in form to be considered as minor variations of the same organism. Members of the group normally interbreed and reproduce their own kind over considerable periods of time." (Trueman 1979)

"A species is a diagnosable cluster of individuals within which there is a parental pattern of ancestry and descent, beyond which there is not, and which exhibits a pattern of phylogenetic ancestry and descent among units of like kind." (Eldredge & Cracraft 1980)

"Species are simply the smallest detected samples of self-perpetuating organisms that have unique sets of characters." (Nelson & Platnick 1981)

"Each species is an internally similar part of a phylogenetic tree." (Willis 1981)

"We can, therefore, regard as a species that most inclusive population of individual biparental organisms which share a common fertilization system." (Paterson 1985)

"An 'evolutionary species' is a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate." (Wiley 1978)

"A species is what a good taxonomist says it is." (Anon.)

TABLE 1 *continued*

"At the outset I confess a disbelief in species, as that word is commonly understood to refer to the basic taxonomic unit or to the taxonomic unit of evolution . . . There seem to be no basic taxonomic units and no particular taxonomic unit of evolution . . . and as Agassiz said in 1859 'species do not exist in nature in a different way from the higher groups'." (Nelson 1989)

"... species as the most inclusive group of organisms having the potential for genetic and/or demographic exchangeability." (Templeton 1989)

A species is "the smallest aggregation of populations (sexual) or lineages (asexual) diagnosable by a unique combination of character states in comparable individuals (semaphoronts)". (Nixon & Wheeler 1990)

Species "refer to groups of actually or potentially interbreeding populations isolated by intrinsic reproductive barriers from other such groups. Evidence for reproductive barriers . . . will involve concordant genetic differences among the populations involved". "Subspecies are groups of actually or potentially interbreeding populations phylogenetically distinguishable from, but reproductively compatible with, other such groups. Importantly, the evidence for phylogenetic distinction must normally come from the concordant distributions of multiple, independent, genetically based traits." (Avice & Ball 1990)

"Species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups." (Mayr 1942)

"A species is a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature." (Mayr 1982)

"A species is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent." (Cracraft 1983)

Species are "lineages whose components (if distinguishable) are not incontrovertibly on different phylogenetic trajectories (i.e. sublineages, if distinguishable, are reproductively compatible), as long as these sublineages do not form a paraphyletic group in recovered history". "The species category . . . would represent the largest entities that *have evolved* whose parts, if distinguishable, are not likely to be on different phylogenetic trajectories." (Frost & Hillis 1990)

"if a given historical group of hybridogens is persistent and is not affecting the evolutionary trajectory of its Mendelian ancestor (as indicated by biogeography, habitat preferences, or genetic divergence), it should be considered a separate species." (Echelle 1990)

A species is the "smallest recognizable monophyletic or unresolved unit". (Donoghue 1985)

"Phylogenetic species can be delimited by a procedure (population aggregation analysis) that involves a search for fixed differences among local populations, followed by successive rounds of aggregation of populations and previously aggregated population groups that are not distinct from each other." "descent relationships among [phylogenetic species] must be hierarchic." (Davis & Nixon 1992)

observing birds from differentiated groups that interact in sympatry, one can determine if they mate assortatively. Because we observe the birds themselves choosing mates, this is deemed 'biological'. However, there is nothing 'non-biological' about the evolution of groups of individuals, the hallmark of the PSC, and the BSC cannot make a claim to be uniquely biological. Perhaps the 'B' in 'BSC' should stand for behavioural.

TABLE 2

Perceived strengths and weaknesses of the biological species concept (see Cracraft 1983, McKittrick & Zink 1988, Zink & McKittrick 1995, Zink 1996b)

Perceived strengths

- Reproductive isolating mechanisms objective in sympatry
- Reproductive isolation = genetic closure of a lineage

Perceived weaknesses

- Amount of hybridization required for conspecificity is vague
- Stable hybrid zones are difficult to assess
- Time to fusion is potentially enormous
- Allopatric populations are judged subjectively
- Evidence of evolutionary pattern is "overruled" by actual or presumed interbreeding
- Non-historical species result because hybridization is not limited to sister taxa
- Reproductive isolation is an epiphenomenon, not a directly measured characteristic of allopatric populations

TABLE 3

Perceived strengths and weaknesses of a Phylogenetic Species Concept

Perceived strengths

- Species limits are consistent with recovered phylogenetic patterns
- Same procedures used for species limits as for higher taxonomic categories
- Based directly on character variation, not an epiphenomenon such as mate choice
- Better description of spatial patterns of biodiversity
- Produces units required by evolutionary theories and conservation biology

Perceived weaknesses

- Lower limits of species require careful study of variation
- Limits of diagnosability problematic
- Too many species will result
- Species might be too ephemeral

The crux of the BSC is that species are reproductively isolated—they have reached that stage in evolutionary divergence where members no longer recognize individuals in other species as mates, or if they do, their offspring are of reduced fitness. Conversely, taxa that are reproductively compatible, especially if they interact in sympatry and form a hybrid swarm, are considered to be conspecific. Thus, the *process* of mate choice is accorded primary significance in determining whether two taxa are to be considered one or two species. This view has intuitive appeal, although I believe that the theoretical and practical flaws with the BSC are insurmountable.

One might argue that in practice the BSC cannot be deemed of primary significance because taxonomists working with some of the most speciose groups actually do not appear to use it. It would be hard to argue (see Whittimore 1993) that botanists use the BSC when delimiting species, given the propensity of plants to hybridize. Similarly, it is doubtful if entomologists (perhaps excluding

lepidopterists) use the BSC, depending instead on morphological differences to recognize most species boundaries. If botanists and entomologists do not generally apply the BSC when describing species, it follows that the bulk of the world's biodiversity is classified primarily by a non-BSC paradigm.

Controversy has surrounded the BSC since its inception (Donoghue 1985, Mallet 1995), although many believe that it has survived the tests of time (Coyne *et al.* 1988). Many problems with using the BSC are familiar (Cracraft 1983), such as the need to speculate whether allopatric populations are reproductively isolated (e.g. Thompson 1991). Zink & McKittrick (1995) reviewed how the significance of hybridization has been misconstrued by proponents of the BSC. It has been implied that hybridization might 'erase' evolved differences between two taxa. However, fusion of hybridizing taxa will likely require long time periods (Zink & McKittrick 1995). Thus, the BSC has been criticized, rightly in my opinion, for basing species limits on what might happen in the future rather than what has happened during the evolutionary past (Cracraft 1983).

The primary new criticism of the BSC to emerge from the writings of phylogenetic systematists is the recognition that reproductive isolation often does not evolve concomitantly with characters that delimit evolutionary taxa, especially in the early stages of divergence. Within many biological species we can recognize separate evolutionary groups, and analyses of their relationships can suggest a pattern that is inconsistent with the pattern of reproductive compatibility—i.e., two hybridizing taxa might not be each other's nearest relatives. A 'species' consisting of two or more groups that are not each other's nearest relatives is unacceptable to modern systematists. In systematics terms, reproductive compatibility is an ancestral condition, because individuals in the ancestral population recognized each other as mates (Rosen 1979). To use the primitive ability to hybridize (perceived in allopatry or documented in sympatry) as a grouping criterion for species limits, as the BSC requires, violates the way in which systematists unite taxa in an evolutionary manner—by possession of shared-derived (i.e. non-ancestral) characters (Rosen 1979). Species limits based on reproductive compatibility (BSC) or patterns of character variation (PSC) can conflict and lead to different species limits from the same data set (Frost & Hillis 1990) (see Fox Sparrow *Passerella iliaca* example below).

The above comments do not mean that advocates of a PSC consider reproductive isolation uninteresting or unworthy of study. Indeed, one could argue that without reproductive isolating mechanisms, the world's species diversity would be kept low because taxa could not become sympatric. Reproductive isolation is an inevitable but temporally unpredictable by-product of evolutionary divergence (McKittrick & Zink 1988). At some point in evolutionary divergence, nearly all differentiated taxa are reproductively isolated, and all reproductively isolated taxa are likely to be 'good' phylogenetic species. I suspect that all species concepts recognize reproductively isolated taxa as different species. However, between the time of the emergence of

taxa on their own evolutionary trajectories (as evidenced by characters) and their eventual reproductive isolation, the pattern of reproductive compatibility is an unreliable predictor of historical relationships of taxa. Although recognizing the intrinsic importance of reproductive isolation, users of a PSC choose not to include this information in the delimitation of species (Frost & Hillis 1990). In fact, proper study of the evolution of an attribute such as reproductive isolation requires first that historical patterns among taxa are known (Brooks & McLennan 1990). The potential for non-historical groupings together with the other often-noted problems (e.g. Donoghue 1985) leads to the inevitable conclusion that the BSC should be replaced with a concept that correctly represents history.

Debate continues over how to use information on evolutionary pattern to delimit species. For example, several phylogenetic species concepts exist (Table 1). Davis & Nixon (1992) suggest that the phrase "phylogenetic species concept" is misleading because the point is to delimit terminal taxa *for* phylogenetic analysis, and they describe a process whereby phylogenetic analysis does not play a role in species delimitation. Rather, they show how morphological or molecular character evidence can be used alone to delimit species. Unlike the BSC, characters are not weighted by their presumed role in a process such as mate choice. Nonetheless, common to history-based concepts, including the evolutionary species concept (Wiley 1978), is the (1) rejection of reproductive compatibility as the primary criterion of conspecific status, and (2) recognition that species can hybridize owing to the retention of the ancestral ability to do so. In my opinion, the crux of a phylogenetic species concept is to recognize groups of individuals that have been on independent evolutionary trajectories. Evaluation of multiple characters does not allow further subdivision of such groups. That is, a PSC attempts to recognize the *status quo*—character analysis reveals groups of individuals that qualify as basal evolutionary units (Cracraft 1983, 1989). Nonetheless, ongoing debate revolves around how best to recognize history at the population level (Davis & Nixon 1992, Zink & McKittrick 1995).

Several criticisms of phylogenetic species concepts exist. Avise & Ball (1990) suggested that with modern molecular methods, each individual would be diagnosable, and might qualify as a separate phylogenetic species. Indeed, if one studied individual gene genealogies (i.e. single characters), one would likely be able to circumscribe groups of individuals on a gene-by-gene basis that are not mutually exclusive, historical entities (see Maddison 1995). One might then think they are forced to recognize individual organisms as phylogenetic species to escape the problem raised by conflicting gene genealogies. However, the opposite trend is actually true. One uses multiple (unweighted) characters and resolves conflicts by an explicit *a priori* criterion (e.g. Davis & Nixon 1992). Species limits are set where character evidence becomes maximally congruent. Some character conflicts might remain, as they do in most phylogenetic studies. Thus, rather than species being single individuals, species often will become geographically coherent groupings of individuals. Resolution of conflicting character

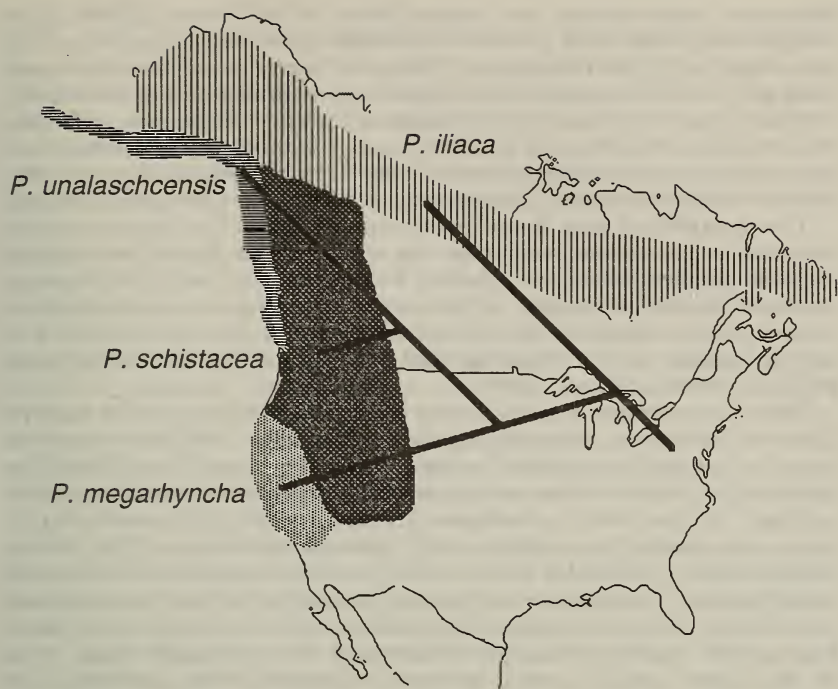


Figure 1. Approximate breeding distribution of four phylogenetic species of the Fox Sparrow *Passerella iliaca*. Phylogenetic tree derived from pattern of restriction sites (Zink 1994).

distributions (e.g. gene genealogies) results in more, not less, inclusive groupings of individuals. The mistaken belief that advocates of a phylogenetic species concept rely on single characters to delimit species has misled several authors (e.g. Amadon & Short 1992). Put another way, a problem with avian subspecies is that they are often based on single characters, and analysis of other characters can suggest different subspecific limits (see below). No taxonomic category, species or otherwise, will likely be based on single characters (Barrowclough 1982).

Differences between biological and phylogenetic species concepts are illustrated by studies of the Fox Sparrow *Passerella iliaca*. In North America, Fox Sparrows range over the taiga, northwest coast, and mountainous regions of the west (Fig. 1). There is considerable phenotypic variation, partitioned by taxonomists into 18 subspecies. However, four basic groups exist: *iliaca*, *unalaschcensis*, *megarhyncha*, and *schistacea*. Each of the four groups was originally recognized as a separate species. The Fox Sparrow is currently considered a single biological species because each group is known to hybridize with at least one other group, although only a few hybrid specimens between

iliaca and *unalaschcensis* are known (Zink & McKittrick 1995). Zink (1994) found that each of the four groups possessed a distinct set of mitochondrial DNA haplotypes. Thus, both genetic and morphological evidence reveal four groups of individuals with separate evolutionary histories—hence, four likely phylogenetic species. (Note that molecular analysis did not indicate a greater number of taxa than that apparent from morphological comparisons.) Zink (1994) suggested, however, that further study of morphology was needed to test and refine species limits.

The question of how many biological species of Fox Sparrow exist depends on how one interprets the evidence on hybridization. An extreme view supports one species, because at least a trickle of genes links all parapatric forms. A moderate view might envisage three species, *iliaca*, *unalaschcensis*, and (*megarhyncha* plus *schistacea*). The latter grouping would obtain because of a narrow hybrid zone between the latter two taxa (Zink 1994).

The main problem in interpreting biological species limits in the Fox Sparrow concerns *megarhyncha* and *schistacea*. MtDNA evidence reveals a narrow hybrid zone between the two groups (Zink 1994). The zone seems broader when morphometric patterns are considered. The stability of the zone is unknown, a factor critical in interpreting biological species limits (Mayr 1982, Zink & McKittrick 1995). If the hybrid zone was stable, Mayr (1982) would consider *schistacea* and *megarhyncha* to represent two species because there was an unknown barrier to complete introgression despite random mating in the zone. Because the zone appears to be between two non-sister taxa, it is probably one of secondary contact (Cracraft 1989) between two phylogenetic species that have retained the primitive ability to hybridize. This study therefore illustrates the problem identified with the BSC by phylogenetic systematists (e.g. Rosen 1979); other avian examples are found in Moore *et al.* (1991) and Freeman & Zink (1995). Lumping *schistacea* and *megarhyncha* into a single species would mis-represent evolutionary history, because although they hybridize extensively, they are not each other's nearest relatives (Fig. 1). It could take tens of thousands of generations for significant introgression to occur (Zink & McKittrick 1995). The PSC would recognize the *status quo*, namely that these two taxa have had independent evolutionary histories and are therefore (phylogenetic) species. Biological species limits depend on one's interpretation of how much (or little) hybridization is required. BSC advocates could therefore recognize 1, 2, 3, or 4 species (which should challenge the belief of those who think that species are real entities of nature). However, a non-historical species including only *megarhyncha* and *schistacea*, permissible under the BSC, would be of no intrinsic value in phylogeny studies, speciation research, biogeography, comparative biology or conservation. I can think of few studies that would intentionally use this classification. Non-historical taxa, then, are the Achilles heel of the BSC.

It is worth noting that the inconsistent relationship between patterns of evolution among populations and their reproductive isolation has only recently been recognized, in part owing to molecular systematics. Molecular methods, such as DNA sequencing, can resolve evolutionary

relationships over short evolutionary time scales, such as within biological species. Prior to molecular analysis, relatively little attention focused on phylogenetic relationships among, for example, subspecies (including those in the Fox Sparrow). Molecular studies can, of course, reveal taxa 'invisible' to morphologists, but more often they elucidate inter-relationships of closely related taxa. Thus, the BSC was invented and used commonly before it was realized that hybridizing taxa might not be sister taxa, and that the pattern of hybridization might misrepresent the true pattern of evolutionary history. Now, however, molecular phylogenetic analysis and classification (i.e. cladistic) methods that require taxonomic boundaries to be faithful to evolutionary ones, mean that the BSC is not an appropriate species concept.

Given the historical usage of the BSC in ornithology, one might wonder if it can be salvaged. The BSC would be improved if subspecies were phylogenetic species that were not reproductively isolated. Species would be required to be consistent with recovered patterns of history (thus, the 'Fox Sparrow' would be either one, two or four species, but one would not accept a species consisting solely of *megarhyncha* and *schistacea* given the pattern of history suggested in Fig. 1). Notwithstanding potential improvements to the BSC, 'species' would still contain variable numbers of basal evolutionary taxa, and thus not be comparable. Also species membership of allopatric subspecies would be judged subjectively, and still one would have to guess whether an allopatric taxon was reproductively isolated rather than emphasizing directly observable character variation. I think that scientific studies require more of species concepts than can be accomplished by re-modelling the BSC.

Implementation of a phylogenetic species concept would remove another contentious area from avian systematics, the subspecies category. Many practising avian taxonomists have in mind a certain 'level of distinctness' required to elevate a subspecies to species; unfortunately, this level varies from taxonomist to taxonomist because of subjective character weighting. Under a PSC, there is no need for the subspecies category (McKittrick & Zink 1988). I suggest that this would be beneficial because of the many avian subspecies that represent arbitrary divisions of clines, or are based on characters not supported by, or conflicting with, other characters. Thus, there would be a single taxonomic category for basal evolutionary taxa—phylogenetic species.

Mayr (1993) was concerned that implementation of a PSC would double the number of biological species of birds (*c.* 9000) recognized worldwide. Mayr implied that this number of species would hinder ornithological research. If this were so, botanists and entomologists surely would be unable to conduct research. G. F. Barrowclough, J. Cracraft & R. M. Zink (unpubl. data) estimated that *c.* 18,000 species of birds exist, using the PSC. This estimate was reached by evaluating morphological evidence that was gathered by previous avian taxonomists for subspecies designations; in fact, many subspecies did not qualify as phylogenetic species (see Hazevoet 1996). This number of species can hardly be perceived as a negative aspect of a PSC (Cracraft 1992). I suggest that it would (1) more accurately portray

avian species diversity (Moritz 1994, Rojas 1992, Cracraft 1997), and (2) put the assessment of avian biodiversity on a more comparable footing with other groups of organisms.

Martin (1996) suggested that use of molecular methods would drastically inflate the number of avian phylogenetic species, many of which would be recognizable only with sophisticated molecular tools (i.e. beyond field identification). Zink (1996a) suggested that the number of new species that were diagnosable only through molecular analyses would in fact be relatively low, and that most taxa supported by molecular analyses also have morphological characteristics (Zink *et al.* 1995). The doubling of the number of bird species mentioned above (G. F. Barrowclough *et al.*, unpubl. data) was based solely on morphological criteria. At the Linnean symposium from which this paper derives, two independent speakers estimated the number of phylogenetic species for particular areas by examination of published (morphological) taxonomies. Thus, I doubt that molecular analyses will reveal many species that are 'invisible' to field workers (see the Fox Sparrow example above), and even if they did, would we recognize as valid components of our biodiversity only those taxa that could be identified with binoculars and a certain level of expertise?

A phylogenetic species concept would also benefit conservation biology (Cracraft 1997). Today, under the BSC, one needs to argue that sometimes local populations, subspecies, or species are units that should be targeted for conservation efforts. In my opinion, many non-systematists (and systematists) view this inconsistency as unscientific. Under a phylogenetic species concept, phylogenetic species would become the category for conservation biology. The explicit goal would be to preserve biodiversity at its most basic spatial scale. It might be thought that some phylogenetic species, formerly 'only' subspecies, would be indefensible for conservation efforts. Because conservation efforts are likely to move from the level of individual species to communities, patterns of species diversity will be used to define conservation entities, such as reserves that capture the bulk of areas of endemism. Spatial patterns of species diversity are most consistently and precisely described under a PSC.

Is the species debate important? Clearly, if different species concepts lead to different species limits given the same data, the answer is yes. The species debate is not a semantic battle between cladists and evolutionary taxonomists. Many researchers are studying speciation. If we cannot agree on a concept of species, how can speciation be effectively studied (Zink 1996b)? If we are discussing how to preserve biodiversity, and species are our measure, species concepts are extremely important. If we use species in evolutionary theories, or comparative studies (Brooks & McLennan 1990), we must be in agreement about how they are described. We must understand properties of species under differing concepts and determine that these properties are what our theories and uses of species require. Researchers should recognize the impact that different species concepts can have on their research, and explicitly consider whether their research programme depends on which concept is used.

Today, the seemingly perennial species debate has been materially changed by contributions from phylogenetic systematics, and has come to involve whether to represent evolutionary history faithfully by species limits. I think that the BSC is theoretically flawed because it can lead to, and accept, misleading historical groupings, and because there has not been a satisfactory resolution to the problem of classifying allopatric populations. Problems with a PSC involve mainly practical ones, such as how to delimit basal taxa, an impressive start at which was made by Davis & Nixon (1992). Although there will be phylogenetic species whose limits are 'fuzzy' owing to the dynamic nature of evolutionary change, and specific individuals difficult to place into a particular species, I think that these problems are far less important than the theoretical and practical ones encountered by applying the BSC. Giving primacy to correct representation of history should be the basis of our species concept, and it will produce species that are best (not perfectly) suited to the majority of biological uses to which they are put. A species concept consistent with a phylogenetic species concept should be adopted in ornithology, replacing the BSC.

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Summary

The debate over species concepts is in an active phase. After years of acceptance of the biological species concept (BSC) in ornithology and other disciplines, the field of phylogenetic systematics has contributed a significant new challenge. Reproductive isolation, the hallmark of the evolution of biological species, does not necessarily evolve in concert with characters that reflect the pattern of population subdivision. That is, taxa on independent evolutionary trajectories, only some of which might be reproductively isolated, can exist within biological species. Therefore, setting species limits consistent with patterns of reproductive compatibility can lead to species limits that misrepresent evolutionary history because hybridizing taxa might not be each other's nearest relatives. A phylogenetic species concept (PSC) equates species with groups of evolutionarily distinct groups of individuals that cannot be further subdivided by analysis of multiple characters, irrespective of mating tendencies. It requires that species limits are consistent with known patterns of evolutionary history. The PSC recognizes that (phylogenetic) species can hybridize because they retain the primitive ability to do so. The debate over species concepts currently focuses on whether to give primary emphasis to reproductive isolation and the process of mate choice (BSC), or to historical patterns of character variation (PSC); this distinction results in different species concepts leading to different species limits given the same data, such as in the example discussed of the Fox Sparrow *Passerella iliaca*. I suggest that a version of the PSC should replace the biological species concept. This would serve several useful functions, such as (1) making species of birds more equivalent with species in other major taxonomic groups, (2) providing an objective method for classifying allopatric populations, (3) removing the contentious category of subspecies, and (4) ensuring that species limits are consistent with recovered historical patterns. Fears that a PSC coupled with molecular methods would produce too many species are unfounded. The units required by phylogenetic analyses, comparative ethological, evolutionary and ecological studies, biogeography, and conservation biology are in practice phylogenetic species; biological species can fail these needs.

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